How do lizards determine dominance? Applying ranking algorithms to animal social behaviour

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Dominance relationships are a defining feature of the social organization of many animal species. Populations structured by absolute dominance usually maintain a generally linear hierarchy, while relative dominance occurs, for example, within territorial populations where an animal is likely to be dominant within its territory. Because relative dominance is dependent on social context, the traits associated with it are often unclear. Green anole lizards, *Anolis carolinensis*, are an ideal system in which to determine dominance-related traits, as anoles use territorial defence in most natural environments, but establish a dominance hierarchy at high densities such as those that occur in captivity. We hypothesized that anoles use similar morphological and behavioural traits to determine social status under both forms of social organization. To test this, we studied a natural population of anoles to determine the traits most predictive of male territory size and quality (as measured by the number of females overlapping a male's territory). While these measures of territory may be related, they measure different components of territorial success. We then used mathematical ranking algorithms to quantify dominance in a tournament of paired arena trials, and identified traits associated with rank. Our results showed that lizards with wider heads had higher social rank, while those with longer heads were more successful at territorial defence. We also found that, independently of morphology, lizards who behaved more aggressively ranked higher in dominance trials, although behaviour did not predict measures of territory. Together, our results indicate that different traits may determine absolute and relative dominance in the green anole.

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Conflicts arise in animal populations when individuals compete for limited resources, such as food, mates or refuges. Physical confrontations between individuals are energetically expensive (Neat, Taylor, & Huntingford, 1998) and potentially dangerous (Clutton-Brock, Albon, Gibson, & Guinness, 1979), so animals of many species use social behaviours to determine resource distribution without frequent fighting. These interactions often involve ritualized displays of size, strength or quality, by which individuals compete to establish social status or dominance over their opponents (Ryan, 1985; Senar, 2006). In populations in which dominance has been established, animals with higher status gain priority access to valuable resources (Kaufmann, 1983) and often experience increased reproductive success (e.g. Schubert et al., 2007; Wroblewski et al., 2009).

Kaufmann (1983) described two broad classifications of dominance: absolute and relative. In populations with absolute dominance, individuals compete to determine their rank in a generally linear hierarchy. Once established, animal interactions are determined by these absolute rankings, regardless of the time or location of future competitions. Even so, strictly linear hierarchies are rare in nature, and most observed hierarchies have some cyclic (i.e. nontransitive) relationships (for example, where A is dominant to B and B is dominant to C, but C is dominant to A; Shizuka & McDonald, 2012). In contrast, in species governed by relative dominance, relationships among individuals predictably change based on when and where competitions occur. Territorial species provide an example of relative dominance, as these animals are more likely to win interactions occurring on their own territories (e.g. Johnsson, Nobbelin, & Bohlin, 1999; Takeuchi & Honda, 2009; Tobias, 1997).

Absolute and relative dominance are often considered to be mutually exclusive (Maher & Lott, 1995), such that a single population may experience only one of the two forms of dominance. For

example, it is generally assumed that territorial animals only know their social rank in relation to their neighbours, as they do not have direct information on the relative fighting ability of individuals they have not yet encountered (Stamps, 1994). Yet, when natural hierarchies form, it is rare that interactions occur between all pairs of individuals; animals may instead infer their position in an overall hierarchy using feedback from interactions within a subset of the population (Hobson & DeDeo, 2015). Whether a population is structured by absolute or relative dominance, individual animals generally rely on the use of display and/or fighting behaviours to establish social status, and they require pairwise comparisons to determine their relative ranks. In this study, we sought to determine the nature of the relationship between these two modes of social organization. Are they independent, maintained by similar behaviours but favouring different traits? Or are they associated, such that an animal's potential position in a dominance hierarchy (in a laboratory environment) is related to the size and/or quality of its territory (in the field)?

We addressed these questions by examining social behaviour in the green anole lizard, *Anolis carolinensis*. Green anoles have become model organisms in the study of behaviour in the field and laboratory, particularly regarding social and reproductive behaviours (reviewed in Crews & Gans, 1992; Greenberg, 1994, 2003; Greenberg et al., 1989; Jenssen, Lovern, & Congdon, 2001; Lovern, Holmes, & Wade, 2004; Wade, 2012). Green anoles of both sexes, but most commonly males, generally defend territories against same-sex rivals (e.g. Jenssen & Nunez, 1998), and thus they predominantly utilize relative dominance in maintaining social networks. However, in particularly dense populations (e.g. those sustained in captivity), male green anoles will forgo territorial defence and instead establish a dominance hierarchy (reviewed in Alberts, 1994; Stamps, 1977). In both the laboratory and field, anoles use the same series of well-described ritualized displays to defend territories and/or establish dominance (Decourcy & Jenssen, 1994; Greenberg, 1977, 2003; Greenberg & Noble, 1944; Jenssen, 1977; Jenssen, Greenberg, & Hovde, 1995). In brief, most aggressive displays between male green anoles usually begin with both individuals performing a series of dynamic displays including push-ups, headbobs and extension of a throat fan called a dewlap. If the interaction continues to escalate, the lizards may move closer together, aligning their bodies in parallel as they begin to circle one another. Static display modifiers such as the development of eyespots, raising a nuchal crest, dorsolateral compression and changing body colour between green and brown may further signal enhanced aggression. Body colour may also indicate stress (particularly if a lizard has brown or blotchy coloration), which can further influence competitive interactions. (While different components of display behaviours are commonly performed together, both the dynamic displays and the static modifiers may also occur on their own.) Ultimately, in the most aggressive encounters, the lizards may 'lock jaws' and attempt to throw each other off the perch. At any point during an interaction, an individual may cease to display or withdraw from the area, thus conceding dominant status to his opponent.

In addition to these behavioural displays of aggression that may establish or maintain dominance, several morphological traits have been shown to predict territorial success and social rank in anoles. In particular, previous studies have suggested that male anole body size is positively associated with territory size and quality (reviewed in Losos, 2009) and dominance rank (e.g. Tokarz, 1985). Social dominance has also been linked to head size (a trait closely related to bite force; Henningsen & Irschick, 2012; Perry, LeVering, Girard, & Garland, 2004), locomotor ability (Lailvaux, Herrel, VanHooydonck, Meyers, & Irschick, 2004; Perry et al., 2004), dewlap size (Lailvaux et al., 2004; Vanhooydonck, Herrel, Van

Damme, & Irschick, 2005) and eyespot development (Larson & Summers, 2001) in laboratory studies of anoles; and tail length is a status symbol in several iguanid lizards (Cooper, 2003; Fox, Heger, & Delay, 1990).

In this study, we sought to determine the morphological and behavioural traits associated with relative (territorial) and absolute (hierarchical) dominance in male green anoles. We used two field measures of territorial success to assess relative dominance: territory size and quality (as determined by the number of females overlapping a male's territory). To quantify absolute dominance, we adapted ranking algorithms developed in the context of sports tournaments to describe the outcomes of a series of paired encounters in a captive population of anoles. Using these measures, we tested the hypothesis that male green anoles use the same combination of these behavioural and morphological traits to determine territory size, territory quality, and social rank. In particular, we predicted that all three measures of social status would be positively related to body size, a trait previously associated with dominance in both laboratory and field settings.

METHODS

Quantifying Territorial Behaviour in a Field Population

Morphological measurements and behavioural observations

We established a 35 × 25 m study plot in Palmetto State Park, Gonzales, Texas, U.S.A. in a seasonal swamp dominated by dwarf palmettos (*Sabal minor*). Between 29 May and 12 June 2013 (i.e. in the middle of the green anole breeding season), we caught 73 adult green anoles (33 males, snout–vent length (SVL) > 55 mm; 40 females, SVL > 45 mm) in the plot by hand or noose. Upon capture, we marked each lizard by sewing a unique bead tag into the tail musculature using surgical wire (Fisher & Muth, 1989). For each male, we also performed a series of morphological measurements. We measured SVL and tail length to the nearest 1 mm, and mass to the nearest 0.1 g. Head length, head width, and dewlap length were all measured to the nearest 0.1 mm using digital callipers, as follows. Head length was measured as the distance from the parietal eye to the tip of the snout, and head width was measured at the widest part of the skull (the anterior base of the cranium). Dewlap length, a proxy for dewlap size (Johnson & Wade, 2010), was measured from the insertion point of the second ceratobranchial cartilage (the cartilage that lines the exterior of the extended dewlap) in the lower jaw to the distal end of the cartilage at the abdomen. After measurements and/or marking were completed, we released the lizard at its site of capture.

After a minimum of 24 h postcapture, we conducted behavioural observations on marked male lizards. Over 3 weeks, we performed 5–30 min focal behavioural observations (average = 24.2 min) on individual males between 0900 and 1700 hours, attempting to observe all lizards across the daily time frame. During observations, we recorded all social behaviours, focusing on the number of dewlap extensions and push-up displays performed. Each lizard was observed for a maximum of 3 h, with multiple observations of an individual lizard separated by at least 2 h. All lizards with a minimum of 2 h of observation, and those that were observed in a minimum of four observations, were included in subsequent analyses.

Territory measurements

To estimate lizard territories, we established reference points throughout the study plot. Each time a marked lizard was sighted, we measured the distance from the lizard's perch to the closest reference point using measuring tape, and the angle from north between the two points to the nearest degree using a compass. In

addition, after each behavioural observation, we measured the location of one to three perches that encompassed the area occupied by the lizard during the observation. Because anoles generally defend all of the area that they use, the territory of these animals is frequently considered to be equivalent to their home range (reviewed in Losos, 2009), and so we used all sightings of each lizard in our calculation of territory size.

We calculated each male's territory size by first converting the location data into planar Cartesian coordinates. We used these coordinates to compute the 95% minimum convex polygon (MCP; Rose, 1982) for each lizard, using the mcp function in the 'adehabitatHR' package (Calenge, 2006) in R (R Core Team, 2014). All males that met the behavioural observation criteria described above also exceeded the minimum number of sightings ($N = 5$) required to estimate territory size using MCPs (range 9–51 sightings per male, mean = 24.9).

We calculated the total number of females living within each male's territory, sensu Johnson, Revell, and Losos (2010), as a measure of male territory quality. To achieve this, we first generated polygons that represented the locations of each female's territory. For all females with five or more sightings ($N = 25$), we performed MCP analysis in R as described above. If a female had three or four sightings ($N = 8$), we used the polygon created by connecting these points to locate its territory. For those females with only one or two sightings ($N = 8$), we added ±0.05 m to the observed point(s) (a value within the error in our field measurements of the distance between a perch and the closest reference point) to generate enough points to create a polygon that would serve as a proxy for its territory. We then created a code in R to count the number of female polygons that overlapped each male MCP, using the package 'plyr' (Wickham, 2011).

Data analysis

Because mass, head length, and head width were correlated with body size, we regressed these variables against SVL and used standardized residuals as a relative measure for each variable in subsequent analyses. Dewlap length and tail length did not correlate with SVL and were thus included in analyses without transformation. Using a stepwise model selection analysis for each of the two measures of male territories (territory size and female overlap), we determined the relationship between the territory measure and seven response variables: SVL, relative mass, relative head width, relative head length, tail length, dewlap length, and total display rate (the sum of the rates of dewlap extensions and push-up displays). When the initial stepwise regression produced a model with nonsignificant components, we considered the Akaike information criterion (AIC) values of models with and without the nonsignificant variables. AIC analyses use a likelihood function to generate a relative measure of how well a model fits a given data set, and are commonly used to compare a set of possible models. Generally, if a given model has an AIC value of two or more units larger than another model, then it is considered a better descriptor of the data, and models within two AIC units are considered to be equally well suited to the data set (Agresti, 2002). In our analyses, if both models were within two AIC units, we selected the model with the fewest number of variables. Otherwise, we chose the full model identified by the stepwise regression. Finally, we used a Pearson correlation test to determine the relationship between the size of a male's territory and the number of females within it. All analyses were performed using R.

Quantifying Social Rank in a Captive Population

Collecting and housing lizards

We captured 20 adult male green anoles by hand or noose from several natural areas in San Antonio, Texas in July (within the summer breeding season) 2012, ensuring that captures were separated by a minimum of 30 m so that lizards in the study would not have had neighbouring territories in their natural habitat. (These were not the same lizards examined in the field study described above.) All lizards were individually housed for 2–3 weeks at Trinity University following established housing and care procedures for anoles (Sanger, Hime, Johnson, Diani, & Losos, 2008). In brief, each lizard was housed in a polycarbonate rodent cage with dimensions $20 \times 21 \times 27$ cm^3. A full spectrum ultraviolet (UV) and heat bulb (Fluker's Sun Spot, Fluker Farms, Port Allen, LA, U.S.A.) was positioned directly over each cage, on a 12:12 h light:dark cycle. We misted each cage daily to provide the lizards with drinking water, and each lizard was fed two crickets on alternating days. Cages were separated by wooden dividers to prevent the lizards from visually interacting.

Arena trials

We designed a tournament of paired arena trials in which each lizard competed in one trial per day for 6 days. The resulting tournament network had a diameter of two; thus, at the end of the 6 days, every lizard i had either encountered lizard j or had a common opponent with lizard j. This tournament design reflects the establishment of natural hierarchies, in which individuals may interact with a subset of a population and then infer their population-level rank from those interactions (Hobson & DeDeo, 2015). We randomly assigned the 20 male lizards identification numbers (1–20) and marked each lizard's number on its dorsum to allow easy identification by observers during the trials.

Before each trial, we placed the two lizards under opaque plastic containers ($5 \times 10 \times 7$ cm^3) positioned on opposite sides of a mesh cage ($63 \times 39 \times 37$ cm^3). Because anoles are arboreal and prefer to utilize vertical perches, we placed a single wooden perch between the two containers to provide a resource over which the lizards could compete, following standard procedures for anole dominance trials (e.g. Garland, Hankins, & Huey, 1990; Henningsen & Irschick, 2012; Perry et al., 2004). After a 10 min acclimation period, we removed the containers and the 10 min trial began. Two observers recorded the number of push-ups and dewlap extensions performed, the time at which an eyespot developed, whether a nuchal crest appeared, the time of the first dewlap or push-up display and the time at which the lizard climbed onto the perch. Each observer documented behavioural data for an individual lizard from behind a blind a minimum of 5 m away from the cage. After each trial, the observers agreed upon the winner (i.e. the more dominant animal) and recorded the time during the trial at which they could make this determination (i.e. time to resolution). In most cases, this was the time at which the dominant lizard took the perch. We identified the lizard as the winner if it monopolized the perch, was higher on the perch than the other lizard at the end of the trial, or if the other lizard clearly showed submissive behaviour (e.g. running away or attempting to hide). If the lizards were at the same height on the perch at the end of the trial, did not interact, or attempted to lock jaws, we called the trial a tie. When the lizards attempted to lock jaws, the trial was immediately ended and the lizards separated. In the event of a tie, the time to resolution was recorded as the length of the trial or, for trials with locked jaws, the time to biting. After the trials, we returned the anoles to their home cages and provided them food and water. Two anoles expired before the end of the tournament, and the data from their trials were not included in the ranking analysis (see Ethical Note for more information).

After the arena trial tournament was completed, we collected morphological measurements for each lizard. As described above, we measured SVL, mass, head length and width, dewlap length and tail length.

Calculating rankings

To determine the social hierarchy of the lizards in the arena trial tournament, we used a series of mathematical ranking algorithms to assign each lizard a rank in the population. A ranking algorithm is a method to determine the relative order of a group of objects, which are evaluated in a series of paired comparisons according to some quantitative measure. The use of ranking algorithms allowed us to design an arena trial tournament in which each lizard did not have to interact with every other individual, since these algorithms have been developed for the purpose of ranking units in contexts in which information is incomplete. A complete tournament, in which each of 20 lizards would interact with each other lizard, would have required a total of 190 trials. Yet, by taking advantage of the power of ranking algorithms, our tournament required only 60 trials to achieve a tournament with a diameter of two. There are multiple mathematical approaches to ranking, and because different ranking systems utilize different information about object quality, we used multiple systems to identify the traits associated with rank in green anoles.

Each ranking system can be treated in the same basic mathematical framework. Consider a collection of n objects $(T_1, T_2, \ldots, T_n)$, called teams. For each paired comparison or "game" between two teams, the outcome for a team can be a win, loss or tie. The outcome of each game can also contain information, such as a score, that can be used to determine the quality of the win. The collection of all games is called a tournament. From the tournament, we determine $\mathbf{r} = (r_1, r_2, \ldots, r_n)$ called the rating vector. We interpret r_i as the team's rating and we say that T_i is rated higher than T_j if $r_i > r_j$. We can order the elements of $\mathbf{r}$ to generate the ranking of the tournament, where the team T_i with the largest r_i value is ranked first, the team with the next highest is ranked second, and so on, down to rank n.

We consider A to be the directed (weighted) adjacency matrix associated with the tournament (i.e. network). That is, A is an $n \times n$ matrix where a_{ij} represents the number of times T_i beats T_j, and a tie is weighted as half of a victory. Let $\mathbf{e}$ be the $n \times 1$ vector with all entries equal to one. Then we can define the win and loss vectors $\mathbf{w}$ and ℓ, respectively by $\mathbf{w} = A\mathbf{e}$ and $\ell = A^t\mathbf{e}$.

We can also include the score of games in the associated networks by weighting the edges according to the score of each game. Thus, we consider two weighted adjacency matrices S and S_D called the Scoring and Score Differential matrices, respectively. In this case, we define the entries s_{ij} to be the total score of T_i over T_j in all games played between the teams while $s_{D_{ij}}$ is the total score differential of T_i over T_j, that is, the margin of victory in all games played between the teams.

In the current application of ranking algorithms, we used eight distinct algorithms to find the rating vector $\mathbf{r}$: Win Percentage, Colley, Massey, Bradley–Terry, Keener, Biased Voter, PageRank, and Oracle (reviewed in Balreira, Miceli, & Tegtmeyer, 2014). Each system emphasizes different statistics of the tournaments, games, or competitors, and each uses different mathematical techniques (see Appendix for descriptions of each ranking system). However, we note that some ranking methods (i.e. Biased Voter, PageRank and Oracle) allow customization, and so we adjusted the parameters of these algorithms to reflect our novel application of these methods. In particular, we defined the score of a paired lizard interaction to be $s_{ij} = \frac{600 - t_{R_{ij}}}{100} + 1$ where $t_{R_{ij}}$ is determined by the time to resolution in the game between T_i and T_j and is defined as: (1) for the winner of the trial, the time (in seconds) at which T_i won the trial, (2) for the loser of the trial, 600 (the total seconds in a 10 min trial), (3) in the case of a tie, 600 for both T_i and T_j, or (4) in the case of a lock-jaw fight during a trial, the time (in seconds) at which T_i and T_j attempted to bite each other. Observe that in the case of a tie or a lock-jaw fight, both teams receive the same score.

The computation of the rating vector of each ranking system was performed using MatLab (MathWorks, Natick, MA, U.S.A.) and the 'bradleyterry2' package in R (Turner & Firth, 2012). For subsequent analyses, we used the rating vector as our measure of social rank, such that higher ratings correspond to higher ranks. We compared the rating vectors from multiple ranking systems using pairwise Pearson correlation.

We also calculated the triangle transitivity of the lizard interaction network using R code from Shizuka and McDonald (2012). Transitivity is a measure of the linearity of a hierarchy that describes how often interactions between individuals can be used to predict outcomes of other interactions; for example, if A beats B and B beats C, we expect A to beat C in a transitive network. In this example, if A dominates both B and C, and B dominates C, then the individuals can be ranked as A (most dominant) > B > C (least dominant). A high incidence of transitive triads indicates a large number of linear interactions in the system (Shizuka & McDonald, 2012). Transitivity measures were calculated by determining the number of triads that were transitive in the set of all triads in the network.

Data analysis

Using the rankings calculated from the arena trial tournament, we determined the morphological and behavioural traits associated with lizard social rank. Because of the relatively large number of variables considered (11) and the relatively small number of lizards in the study ($N = 18$), we used a principal component analysis (PCA), performed in SPSS v.19 (IBM, Armonk, NY, U.S.A.), to reduce the number of behavioural variables. The PCA included four correlated measures of behavioural data (rate of dewlap extensions, rate of push-up displays, time to eyespot development and time of first display) and produced one PC with an eigenvalue greater than one. This PC, called behaviour PC, loaded highly for all four of these behavioural variables and described 73% of the variation in the behavioural data (Table 1). The percentage of time an individual raised its nuchal crest (here, called crest) was included in our subsequent analyses separately, as it was not correlated with the other behavioural measures. As above, because mass, head length, and head width were correlated with overall body size, we conducted regressions with these variables against SVL and used standardized residuals in subsequent analyses. Dewlap length and tail length again did not correlate with SVL and were thus included in the analysis without transformation.

For each of the eight ranking systems, we performed a stepwise model selection analysis (as above) to determine associations between the rating vector and the eight response variables (SVL, relative mass, relative head length, relative head width, dewlap length, tail length, behaviour PC and crest).

Ethical Note

The two lizards who expired during the arena trial tournament appeared to have died of natural causes. Early in the tournament,

Table 1

Principal component analysis of correlated behavioural variables from the arena trial tournament

Variable	Loading coefficient
Dewlaps per min	0.911
Push-ups per min	0.907
Time to first display	−0.848
Time to eyespot development	−0.754
Eigenvalue	2.94
% Variation explained	73.5

each of these two lizards were unexpectedly discovered dead in their home cages during our standard morning animal checks. Neither had sustained any injuries during arena trials, both were a uniform (nonblotchy) body colour upon discovery and both had appeared to be well hydrated and healthy on the previous day. On occasion, wild-caught animals suffer mortality in captive conditions, and the deaths of these lizards did not appear to be related to the manipulations of this experiment. Indeed, all other lizards in the study generally maintained a uniform green colour throughout the duration of the study, suggesting that the other lizards were all healthy and experienced relatively low levels of stress in this captive environment.

All procedures were performed in accordance with the guidelines of the Trinity University Animal Use Committee (protocol number 050213_MAJ2) and Texas Parks & Wildlife Scientific Research Permit 0310-045.

RESULTS

Traits Predicting Relative Dominance

Male territories ($N = 24$) overlapped extensively, with 79.2% of males maintaining territories that overlapped the territories of at least three other males and 33.3% of males overlapping at least five neighbouring territories (Fig. 1). All male territories overlapped at least one female (minimum = 1, maximum = 10, mean = 5.2; Fig. 1). Total male territory size was correlated with the number of female territories overlapped ($r_{22} = 0.69$, $P < 0.001$); that is, males with larger overall territories generally had territories of higher quality.

Territory size (MCP) was most strongly associated with relative head length, relative head width and dewlap length (Table 2), such

that males with larger territories had wider, shorter heads and larger dewlaps. Female overlap of male territories (i.e. male territory quality) was also associated with relative head length and relative head width (Table 2), such that males who overlapped more females had wider, shorter heads. Body size (relative mass or SVL), tail length and display behaviour were not associated with territory size or quality in this population (Table 2).

Traits Predicting Absolute Dominance

In our tournament of arena trials, 75% of interaction triads were transitive. This transitivity level was not distinguishable from that expected in a random network (in which transitivity is also predicted to be 75%), indicating that our captive population of anoles established a nonlinear hierarchy. This also indicates that a ranking method based on paired comparisons is more suitable to determine hierarchy than a linear ranking method based on a single score for each individual.

To determine whether different ranking systems would identify similar traits associated with male dominance, we used eight systems in this analysis. The rating vectors produced by the eight algorithms were highly correlated (Table 3), and the morphological and behavioural traits associated with rank were generally consistent across the ranking systems (Table 4). For each system, rank was significantly predicted by at least one measure of behaviour (behaviour PC (Table 1) and/or crest), and ranks resulting from seven of the eight systems were a function of relative head size (greater relative length and/or less relative width). In addition, tail length was negatively associated with rank in four systems, and dewlap length was a significant predictor of rank in the Bradley–Terry system (Table 4). In contrast to our predictions, neither
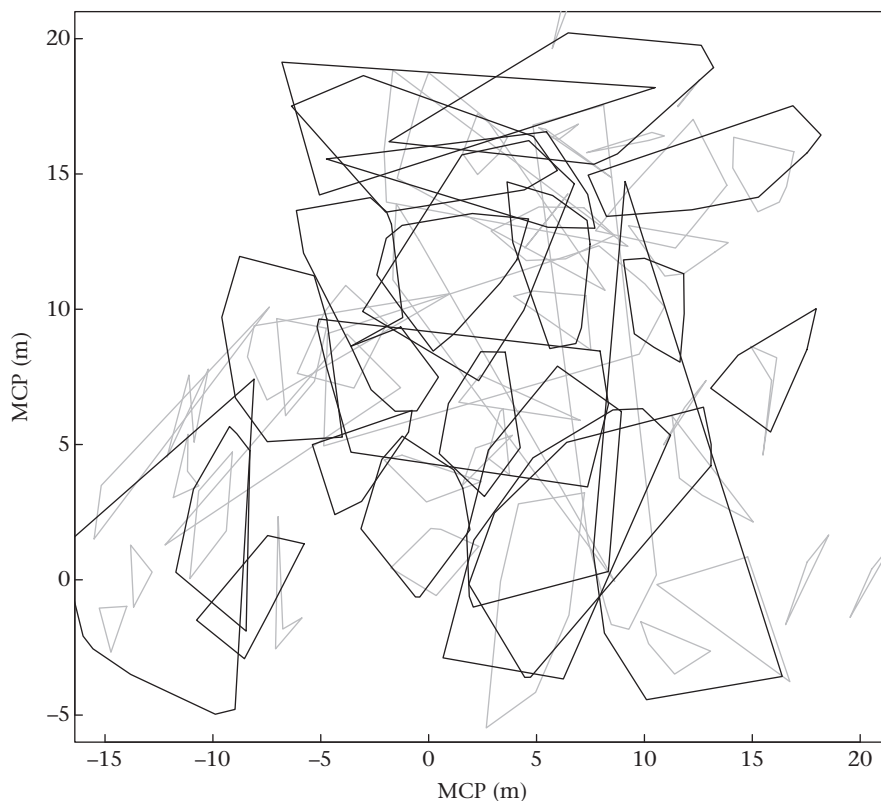
Figure 1. Territories of 64 adult *Anolis carolinensis* in Palmetto State Park, Gonzales, Texas, mapped (in metres) using minimum convex polygons (MCPs). Black polygons represent male territories ($N = 24$), while grey polygons represent female territories ($N = 40$).

Table 2
Traits that predicted male territory size and overlap with female territories in a natural population of green anole lizards

Territory metric	Traits							Adj. R^2
	Rel. head length	Rel. head width	SVL	Rel. mass	Dewlap length	Tail length	Total display rate	
Territory size	−1.32***	0.91**			0.30†			0.43***
Female overlap	−1.10**	1.62†						0.37***

Values indicate the beta coefficients of the most successful combination of traits for a given territory metric, identified using a stepwise model selection analysis. 'Rel.' denotes relative measures (standardized by snout−vent length, SVL). †$P < 0.1$; **$P < 0.01$; ***$P < 0.001$.

Table 3
Pearson correlation values comparing the ranks generated by the different ranking systems

	Win %	Colley	Massey	Bradley−Terry	Keener	Biased voter	PageRank	Oracle
Win %	1.00	0.90	0.64	0.85	0.64	0.76	0.72	0.90
Colley		1.00	0.68	0.96	0.77	0.90	0.84	0.96
Massey			1.00	0.70	0.68	0.73	0.73	0.74
Bradley−Terry				1.00	0.81	0.95	0.86	0.95
Keener					1.00	0.90	0.97	0.86
Biased Voter						1.00	0.92	0.94
PageRank							1.00	0.91
Oracle								1.00

All correlations were significant at $P < 0.01$.

Table 4
Traits that predicted rank in the arena trial tournament in a laboratory population of green anoles

Ranking systems	Traits								Adj. R^2
	Rel. head length	Rel. head width	SVL	Rel. mass	Dewlap length	Tail length	Behavior PC	Crest	
Win %	0.38*						0.60***	0.33*	0.72***
Biased Voter	0.56*	−0.47*					0.51*		0.60**
Keener	0.77*	−0.51*				−0.40*		0.41*	0.57**
Bradley−Terry		−0.42*			0.83**	−0.49*	0.67*		0.49**
Massey						−0.27*	0.68**		0.49*
Colley	0.36**						0.66***	0.38*	0.75***
PageRank	0.61*	−0.35				−0.33*	0.39*	0.34*	0.67**
Oracle	0.35**						0.64***	0.35**	0.80***

Values indicate the beta coefficients of the most successful combinations of traits for a given ranking system, identified using a stepwise model selection analysis. 'Rel.' denotes relative measures (standardized by snout−vent length, SVL). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

measure of body size (relative mass or SVL) was significant in any ranking system.

DISCUSSION

The overall goal of this study was to determine the traits associated with social status in the green anole lizard in two contexts: rank within a dominance hierarchy in a captive population and territorial defence in a natural population. We hypothesized that the same morphological and behavioural traits would predict rank, territory size, and female overlap. Our results suggested that relative head length and width (and not body size) were associated with all three measures, but we found that head shape and behaviour predicted social status in contrasting ways in the two contexts. Thus, we propose that these traits signal different information in different social environments.

In a territorial field population, the relationships that determine social status may be established by interactions over months, or even years (Stamps, 1994), and the intensity and outcomes of these interactions may vary across seasons or years as well. In this study, we found that lizards with shorter, wider heads maintained larger, higher-quality territories (Table 2), suggesting that long-term successful territory defence is likely based on fighting ability, which is directly associated with head shape. Physical combat in anoles consists of "locking jaws," in which two individuals bite each other's jaws and often attempt to throw the other lizard off its perch. Lizards with larger heads, and particularly those with wider and/or deeper heads, generate more force when they bite in agonistic interactions, as these head dimensions allow for increased jaw adductor musculature (Herrel, Grauw, & Lemos-Espinal, 2001; Herrel, Spithoven, Van Damme, & De Vree, 1999; Huyghe, Van-hooydonck, Scheers, Molina-Borja, & Damme, 2005; Vanhooy-donck et al., 2005). Increased bite force may cause greater injury to the opponent, increasing an individual's chance of winning an encounter (Husak, Lappin, Fox, & Lemos-Espinal, 2006). Thus, bite force (Henningsen & Irschick, 2012; Perry et al., 2004) and head size (Perry et al., 2004) have often been identified as important predictors of dominance in anoles. Our findings are consistent with this literature, suggesting that bite force influences an individual's territorial success. Furthermore, in our natural field observations, we observed one lock-jaw fight between two males in our 75 h of observations, suggesting that physical combat is a relatively rare but relevant strategy for territorial defence in this population.

In contrast, we found that dominant individuals in arena trials were more likely to have longer, narrower heads than less dominant lizards (Table 4). This unexpected result may be due to the difference between the social context of the arena trials (in which opponents were given little time or space to evaluate their opponent) and the natural anole interactions in the wild. In close encounters such as those that occurred in the arena trials, lizards usually align their bodies in parallel, an orientation that could make it difficult to gauge an opponent's head width. However, head

length would be clearly visible from this parallel alignment (Jenssen, 1977). Relative head length and width were highly correlated in the present study ($r_{16} = 0.63$, $P = 0.006$), so lizards in the arena trials may have been primarily responding to the absolute head size of their opponent (which is directly associated with bite force; see references above), instead of the relative dimensions that were likely more difficult to assess. In addition, as head length increases, there is an increase in gape distance (Herrel, Van Damme, & De Vree, 1995), which may also be related to successful combat in a lock-jaw fight. Thus, relative head length may function as a visual signal associated with bite force that can be quickly gauged in a close range, short-term interaction.

Furthermore, our results suggest that aggressive behaviour may be more predictive of the outcome of an arena trial than potential bite force (Table 4). Display behaviours (e.g. dewlap extensions, push-up displays, eyespot development and nuchal crest enlargement) signal the likelihood that an individual will engage in physical combat and/or exhibit dominance (Jenssen, 1977; Larson & Summers, 2001; Wilczynski, Black, Salem, & Ezeoke, 2015). In our arena trial tournament, lizards were required to size up their opponents with little social information. In this context, the immediate motivation of the other lizard, as signalled via display behaviour, may be the most critical determinant of such contests.

There are several reasons that behavioural signals may have played a larger role in the artificial conditions of the arena trials than in the natural conditions of the field. First, lizards in their natural environment may have already established a clear network of dominance relationships, and thus behavioural displays to known neighbours may be less critical than those in the arena trials between unknown opponents, especially if behavioural displays in the wild may attract the attention of potential predators. Next, captive lizards may have been more stressed than their wild counterparts, and potentially more likely to display due to that stress. Finally, behavioural displays in the wild occur in a variety of social contexts, including aggression, courtship and predator pursuit deterrence (Leal & Rodríguez-Robles, 1997). Thus the displays observed in the field likely produced multiple signals, while those observed in the controlled environment of the arena trials presumably served the sole function of aggression.

Alternatively, display behaviours may have differed between the field and arena trials because of the low value of the contested resource in the trials (a perch in a space with no prior value to the lizard), as opposed to a territory, a space with high value to the territory holder. For example, Tibbetts (2008) found that in Polistes paper wasps, individuals trusted the signals of an opponent when fighting over a low-value resource, but they were more likely to test the accuracy of an opponent's signal when fighting over a high-value resource. Moreover, O'Connor et al. (2015) recently reported that aggression in a wild cichlid fish (Neolamprologus pulcher) was greatest when competing over high-quality resources, and that aggressive behaviour predicted the results of dominance trials while body size did not. While the current study was not designed to directly test the role of resource value, the results of these studies are consistent with the nontransitive (nonlinear) hierarchy observed in our captive population, in which dominance relationships among the lizards were not solely determined by static morphological traits.

Although head shape and aggressive behaviour were the traits most strongly related to social status in this study, dewlap length and tail length were also identified as potentially important qualities. Dewlap length, a proxy for dewlap size (Johnson & Wade, 2010), had the highest beta coefficient in the Bradley−Terry ranking system (Table 4) and was a marginal predictor of territory size (Table 2). Similarly, signal or ornament size has been shown to be a critical predictor of territorial and dominance status in many taxa. For example, lark buntings, Calamospiza melanocorys, and collared flycatchers, Ficedula albicollis, with larger coloured wing patches have fewer territorial intruders than birds with smaller ornaments (Chaine & Lyon, 2008; Hegyi, Garamszegi, Eens, & Trk, 2008). Furthermore, dewlap size is positively correlated with bite force in some Anolis species (e.g. Henningsen & Irschick, 2012). However, previous experimental reductions of anole dewlap size (Henningsen & Irschick, 2012) or use (Tokarz, Paterson, & McMann, 2003) did not change the dominance outcomes of paired encounters.

Surprisingly, shorter tail length significantly predicted rank in three of the eight ranking systems in the arena trial tournament. Like many lizards, anoles use tail autotomy to avoid predation, and autotomy may also occur during fights with conspecifics. After losing their tails, lizards of many species experience reduced social status (common side-blotched lizard, Uta stansburiana; Fox et al., 1990), smaller territory size (Algerian sand lizard, Psammodromus algirus; Salvador, Martin, & López, 1995), and reduced mating frequency (Iberian rock lizard, Lacerta monticola; Martin & Salvador, 1993). Thus tail length may be a status signal that indicates superior predator avoidance skills, which makes the negative relationship between tail length and dominance in our arena trials difficult to interpret. We offer one possible explanation for this result: since males who fight more frequently may experience more frequent tail autotomy, shorter tails may be related to an individual's propensity to engage in physical combat, a trait associated with dominance in the arena trials (as discussed above).

Finally, in this study neither SVL nor relative mass were significantly related to any measure of absolute or relative dominance. However, larger male body size in anoles has been associated with larger territory size and greater female overlap of male territories (Jenssen & Nunez, 1998; Ruby, 1984; Schoener & Schoener, 1982), and larger male body size is generally assumed to be a likely determinant of dominance in paired encounters. Indeed, after the classic study of dominance and body size in brown anoles, Anolis sagrei, by Tokarz (1985), dominance trials in anoles have commonly used size-matched pairs (e.g. Garland et al., 1990; Henningsen & Irschick, 2012; Perry et al., 2004). Yet Tokarz's (1985) study paired males that differed dramatically in body size (large males had an average SVL of 49.4 mm, while small males had an average SVL of 39.5). In contrast, half of our trials paired lizards that differed in SVL by 3 mm or less and thus can be considered size-matched (e.g. Garland et al., 1990; Henningsen & Irschick, 2012; Perry et al., 2004) and 17 out of the 24 territory holders in our natural population had an SVL between 64 and 67 mm (see Field Data at http://digitalcommons.trinity.edu/bio_faculty/59/). Together, these results suggest that body size may be a status signal that is dependent on context, such that it has a strong effect when individuals differ substantially in length or mass but is of little importance in relatively size-matched pairs. In many social interactions, there may be other morphological and behavioural traits (such as those identified in this study) that are more predictive of social status than body size.

Conclusion

Overall, the results of this study suggest that dominance relationships in the green anole are determined by context-specific criteria. Long-term relationships (as measured by territory size and female overlap in a natural setting) were related to traits that honestly predict fighting ability, while short-term relationships (i.e. those determined by arena trials in a laboratory setting) were more accurately predicted by behaviours signalling immediate intentions. This indicates that even highly stereotyped displays can convey a variety of meanings depending on the situations and the

individuals involved (Greenberg, 2003). Our use of ranking algorithms greatly enhanced our analysis of captive populations, allowing a more elegant study design than would otherwise have been possible and revealing patterns that would not otherwise have been obvious. These algorithms offer an exciting new perspective for quantifying animal behaviour.

Acknowledgments

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APPENDIX. DESCRIPTION OF MATHEMATICAL RANKING ALGORITHMS USED TO DETERMINE LIZARD DOMINANCE

There are many different ranking algorithms developed for network theory and sports ranking applications that emphasize different statistics of the tournaments, games or competitors (Balreira et al., 2014; Langville & Meyer, 2012). A ranking system is a method to determine a rating vector, $\boldsymbol{r} = (r_1, \ldots, r_n)$, for a group of n teams, $\{T_1, T_2, \ldots, T_n\}$. We interpret r_i as the team's rating and we say that T_i is rated higher than T_j if $r_i > r_j$. We can order the elements of $\boldsymbol{r}$ to generate the ranking of the tournament, where the team T_i with the largest r_i value is ranked first, the team with the next highest is ranked second, and so on, down to rank n.

We view the results of the tournament as a network by determining the directed (weighted) adjacency matrix associated with the tournament, to be denoted by A. Thus the matrix A is an $n \times n$ matrix where a_{ij} represents the number of times T_i beats T_j and a tie is weighted as half of a victory and half of loss. Let $\boldsymbol{e}$ be the $n \times 1$ vector with all entries equal to one. Then we can define the win and loss vectors $\boldsymbol{w}$ and ℓ, respectively by $\boldsymbol{w} = A\boldsymbol{e}$ and $\ell = A^t\boldsymbol{e}$. Some ranking methods may also include the scores of games in the associated networks by weighting the edges according to the score of each game. In this case, we consider two weighted adjacency matrices S and S_D called the Scoring and Score Differential matrices, respectively. We define the entries s_{ij} to be the total score of T_i over T_j in all games played between the teams while $s_{D_{ij}}$ is the total score differential of T_i over T_j; that is, the margin of victory in all games played between the teams.

Some ranking methods, such as Colley and Massey find the rating vector $\boldsymbol{r}$ to be the solution of a linear system of equations. Others such as Keener, Biased Voter, PageRank, and Oracle define the rating vector $\boldsymbol{r}$ as the steady state of a Markov process in the associated network where the transitional probabilities are obtained from the weighted adjacency matrix. The existence of the rating vector is guaranteed by the Perron—Frobenious theorem (Horn & Johnson, 1990). Namely, for a matrix with non-negative entries such that its associated network is a strongly connected network, then there exists a positive dominant real eigenvalue, called the Perron—Frobenious eigenvalue with the associated Perron—Frobenious eigenvector. The Perron—Frobenious eigenvector has non-negative entries that can be normalized to sum to one and this is the rating vector associated with the ranking method.

Below, we provide a mathematical description of how each method used in this project was implemented in this study of lizard dominance.

1. Win Percent: This is the simplest ranking algorithm, where rate r_i of a team is a ratio between the number of wins and the total number of games played; that is, $r_i = \frac{w_i}{w_i + \ell_i}$.
2. Colley: In this method developed by Colley (2002), a team's ranking is based on adjusting its win percentage such that it receives more credit for defeating a strong opponent than for defeating a weak opponent, without taking score into consideration. Rank is determined by solving the linear system $C\boldsymbol{r} = \boldsymbol{b}$, where $C = \text{diag}(\boldsymbol{w} + \ell + 2) - (A^t + A)$ and $\boldsymbol{b} = \frac{w - \ell}{2} + 1$.
3. Massey: This method was developed by Massey (1997) with the idea that $r_i - r_j$ is the expected score differential of the game between T_i and T_j. Thus, the rating vector is the least squares solution to a system $M\boldsymbol{r} = \boldsymbol{y}$, where y_i is the total number of points scored against T_i subtracted from the total number of points scored by T_i. To define M, let $\text{diag}(\boldsymbol{v})$ denote the diagonal matrix with diagonal given by the vector $\boldsymbol{v}$ and thus $M = \text{diag}(\boldsymbol{w} + \ell) - (A^t + A)$. To ensure that M has full rank, Massey replaces the last row of M with a row of all ones and $y_n = 0$.

This adds a constraint to the linear system that states that the ratings must sum to zero.

4. Bradley–Terry: This method was introduced by Bradley and Terry (1952) and estimates that the likelihood T_i beats T_j should be $\frac{r_i}{r_i+r_j}$. Then, from the actual observations, one can use maximum likelihood estimates (MLE; Agresti, 2002) to find the rating vector $\boldsymbol{r}$. The existence of the MLE is contingent on the strong connectivity of the associated network as first observed by Ford (1957). This may not always happen in a tournament, particularly if there is a winless or undefeated team. One possible solution for this problem, which we used in the current study, was proposed by Keener (1993). The approach is to use game scores, or strictly positive scores, to estimate the actual likelihoods; that is, $\frac{r_i}{r_i+r_j} \approx \frac{s_{ij}}{s_{ij}+s_{ji}}$.

5. Keener: In this method developed by Keener (1993), one weights the associated network based on the game scores. Keener (1993) defines the matrix K such that

$$k_{ij} = h\left(\frac{s_{ij}+1}{s_{ij}+s_{ji}+2}\right),$$

and,

$$h(x) = \frac{1}{2} + \frac{1}{2}\operatorname{sgn}\left(x - \frac{1}{2}\right)\sqrt{|2x - 1|}.$$

Next, each entry of K is normalized by the number of games each team has played; that is, K is redefined as $[\operatorname{diag}(\boldsymbol{w} + \ell)]^{-1}K$. The rating vector is the probability eigenvector associated with the eigenvalue one of K. In our application of this method, we defined the score of each interaction as the time to resolution, as described in the Methods.

6. Biased Voter: In this method developed by Callaghan, Mucha, and Porter (2007), one considers a biased voter moving around the associated network of the tournament as follows. With a fixed probability $p \in \left(\frac{1}{2}, 1\right)$, if the biased voter is at the node corresponding to T_i, it randomly selects an opponent of T_i, say T_j, and moves to the winner of that match with probability p and moves to the loser of the match with probability $1 - p$. Formally, one defines

$$BV(p) = p(A - \operatorname{diag}(\ell)) + (1 - p)(A^t - \operatorname{diag}(\boldsymbol{w})).$$

This satisfies the Perron–Frobenious theorem, so the rating vector is well defined. In this paper, we used $p = 0.75$ in our computations, as this is the value generally used in applications of sports rankings (Balreira et al., 2014; Callaghan et al., 2007).

7. PageRank: This method was developed by Page, Brin, Motwani, and Winograd (1999) and is an important component of the original Google search engine. It uses the network associated with the tournament, but with several modifications. First, if there are any dangling nodes (i.e. undefeated teams), we replace the corresponding column of A with the vector $\frac{1}{n}\boldsymbol{e}$. Next, one makes the matrix A column stochastic to create the hyperlink matrix H. Now, one chooses $\alpha \in (0, 1)$ and defines the Google matrix to be the convex combination $G_\alpha = \alpha H + (1 - \alpha)\boldsymbol{v}\boldsymbol{e}^T$. The vector $\boldsymbol{v}$ is called a personalization vector and the choice of $\boldsymbol{v} = \frac{1}{n}\boldsymbol{e}$ is the usual PageRank method. In this paper we used $\alpha = 0.85$, which is the reported value originally used in the PageRank method (Langville & Meyer, 2003). The rating vector is found by the Perron–Frobenious theorem.

8. Oracle: This method was recently developed by Balreira et al. (2014) and addresses a flaw encountered when using certain Markov methods to rank a tournament. Namely, when an undefeated team loses to a winless team, the previously winless team rises to near the top of the rankings. The solution proposed by Balreira et al. (2014) is to add a new node to the system, called the Oracle node, and to add edges to and from each team to the Oracle. These edges can be customized to include additional tournament statistics, such as wins and scores. Formally, we have a new incidence matrix

$$\operatorname{Or}(u, d) = \left(\begin{array}{c|c} A & \boldsymbol{d} \\ \hline \boldsymbol{u}^T & 0 \end{array}\right)$$

where the vector $\boldsymbol{u}$ is the up direction vector and the vector $\boldsymbol{d}$ is the down direction vector. If these are positive vectors, then we ensure that the associated network is strongly connected. Hence, the Perron–Frobenious theorem can always be applied to find an Oracle rating vector as a vector in $\mathbb{R}^{n+1}$. To define the rating vector for the original teams, one normalizes the ratings by $\widehat{r}_i = \frac{r_i}{1-r_{n+1}}$. In this paper, we used $\boldsymbol{u} = \boldsymbol{w} + \boldsymbol{e}$ and $\boldsymbol{d} = \boldsymbol{s}$, where s_i is the time to resolution of T_i as defined in the Methods.